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BOOK CHAPTER

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Trophic Interactions in Experimental Marine Ecosystems Perturbed by Oil

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ABSTRACT

Chronic, low-level additions of No. 2 fuel oil were made to three of nine experimental tanks (mean concentration, 180 ppb; range, approximately 60 to 350 ppb) at the Marine Ecosystems Research Laboratory. Laboratory experiments indicated that the dominant phytoplankton species were relatively insensitive to oil at these concentrations but the phytoplankton populations in the ecosystems receiving oil showed a marked increase in biomass and radically different species composition. The evidence suggests that these changes were caused by the reduced grazing pressure in the oiled tanks, where the densities of zooplankton and benthic suspension feeders were markedly lower than in the control tanks. Nutrient studies in control and oiled tanks support this interpretation. Nutrients in control tanks were generally present in excess but were generally limiting for the elevated phytoplankton populations in the oiled tanks. During the 5-month chronic oil addition, the benthic macrofaunal and metazoan meiofaunal populations declined drastically, whereas benthic protozoa (ciliates and Foraminifera) increased considerably, as did benthic diatoms. The increases may be caused by decreased bioturbation, predation, and grazing by the reduced metazoan populations. These effects could not have been predicted from knowledge of the biology and susceptibility to oil of the individual species and emphasize the usefulness of replicated experimental ecosystems in further analysis of such interactions.

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Understanding and predicting the effects of pollutants and other environmental factors on ecosystems from laboratory studies of lethal and sublethal effects on single-species populations are difficult. Interactions at higher levels of organization in the ecosystem (e.g., between and within trophic levels) may amplify, dampen, or even reverse the direct effect of the environmental factor of interest, giving rise to ecosystem effects that could not have been predicted from single-species laboratory studies. This is a frequently advanced rationale for the use of microcosms in ecosystem research (Taub, 1976). Microcosms allow experimental manipulations and replications not possible in the natural ecosystem, thus retaining some of the analytical advantages of simpler laboratory experiments and still providing much of the complexity of nature (Henderson, Smith, and Evans, 1976).

Two examples of such higher level trophic interactions are presented here during low-level chronic additions of No. 2 fuel oil, which resulted in unexpected effects at the ecosystem level.

DESCRIPTION OF FACILITY

The Marine Ecosystems Research Laboratory (MERL), Graduate School of Oceanography, University of Rhode Island, is comprised of 12 experimental ecosystems (microcosms). The cylindrical tanks are 1.8 m in interior diameter and 5.5 m in interior height. At the bottom of each tank is a sediment container with 0.8 m^3 of mud, 0.3 m deep. The sediment contains a *Mediomastus ambiseta—Nucula annulata* macrofauna community collected from Narragansett Bay with a van Veen grab (we attempted to retain as much as possible of the original orientation of the sediment). The 5.0-m water column gives a total water volume of 13 m^3. The water was exchanged for Narragansett Bay (West Passage) water at a rate of 0.3 liter/min, for a turnover time of about 30 days for each tank. A mechanical mixing device provided four 2-hr periods of mixing per day, turbulent enough to totally mix the water column within 15 min. (For a more detailed description, see Pilson et al., 1977, 1979).

The salinity of the microcosms varied from 28 to 32‰, and the temperatures followed those of Narragansett Bay within ~3°C, varying from −2°C in winter to a maximum of 24 to 25°C in July.

The MERL facility differs from other current large-scale microcosm projects in that it combines a benthic and a pelagic community, both initially derived from a natural ecosystem (Narragansett Bay, Rhode Island). This, combined with the mixing provided, allows a natural regeneration of nutrients from the

sediment, thus eliminating the need for intermittent nutrient additions, such as are made in the CEPEX (Takahashi et al., 1977) and Loch Ewe (Gamble, Davies, and Steele, 1977) water-column enclosures, which lack benthos. The turnover of the water is slow enough that events in the water column of the tanks are dominated by the experimental conditions within the microcosms rather than by the quality of the outside input [as is the case for the microcosms described by Henderson, Smith, and Evans (1976) and Notini et al. (1977)]. The slow water flow from Narragansett Bay was intended to provide a continuous seeding with planktonic organisms, including larvae of the macrofauna, and some suspended benthic meio- and microfauna to compensate for the gradual extinction of species in the limited space of the microcosms, predicted by the theory of island biogeography (MacArthur and Wilson, 1967).

The inclusion of the benthic component in the MERL microcosms both allows (because of nutrient regeneration) and requires (because of the longer life spans of the benthic organisms) longer experimental duration (a year or more) than is common in microcosm experiments with captive segments of natural ecosystems.

METHODS

Operation of MERL

The results in this paper derive from an experiment started in August 1976. Until early December, nine experimental ecosystems were operated in parallel. On December 6, a single oil addition of the water-accommodated fraction of No. 2 fuel oil was made to three of the tanks (henceforth referred to as the oiled tanks). The oil levels initially reached 180 ppb but then decreased rapidly to undetectable levels within a month. By early February the oiled tanks were not significantly different from the six other tanks for the parameters measured. The chronic oil addition experiment was started on Feb. 14, 1977, and continued for 5.5 months, with the last oil addition being made on Aug. 1, 1977. After a recovery period of about 2 months, the experiment was terminated in late September to early October 1977 (termination date varied among tanks). During the period of oil addition, three tanks were left as controls and the three oiled tanks were given two additions per week of the water-accommodated fraction of No. 2 fuel oil. The oil levels averaged 180 ppb over the period of oil addition, peaking at about 300 ppb immediately after an addition and gradually decreasing to about 75 ppb before the next addition. The oil was measured as total lipids by gas–liquid chromatography. The fuel oil used was locally

acquired and was roughly 20% aromatics, measured as benzene eluated fraction by silica gel—alumina column chromatography. Further details on the behavior and fate of the added oil can be found in Gearing et al. (1979).

Phytoplankton

Phytoplankton counts and species identification are based on single Sedgwick—Rafter counts of a pooled sample from each tank. All forms were separated to the species level, except nano- and microflagellates, which were counted as groups.

An index of similarity was calculated based on the presence or absence of a species for all combinations of oiled tanks, control tanks, and control vs. oiled tanks, using the simplified index:

$$S = \frac{2C}{A + B}$$

where A is the number of species in one sample, B is the number of species in the other sample, and C is the number of species in common (Odum, 1971). A Shannon index of general diversity ($\overline{H}$) was used:

$$\overline{H} = -\sum P_i \log_{10} P_i$$

where P is the proportion of each species in the total population (Odum, 1971).

Biomass, as chlorophyll a, was determined on replicate subsamples of a pooled sample from each tank, using the fluorometric method of Holm-Hansen et al. (1965). Nutrient analyses were done in triplicate on the Technicon Autoanalyzer, modified according to Friederich and Whitledge (1972).

Zooplankton

Weekly zooplankton counts were based on two pooled vertical tows per tank. Tows were taken with the mixer in action, from the bottom up, one tow on the shaded side and one on the light side of the tank, with a 50-cm-diameter plankton net with a mesh size of 80 μm. We estimate that this sampling removed ~15% of the zooplankton population each week. All animals present were identified to species level or, in the case of meroplanktonic larvae, to phylum or class.

Tunicate Census and Filtering-Rate Measurements

Tunicate population densities in the tanks were roughly estimated from July in-tank photographs. Tunicate filtering rates were measured under static conditions in 600-ml beakers. Animals of varying sizes (0.08 to 5.1 g wet weight) were fed a log-phase culture of *Skeletonema costatum* ($\sim 6 \times 10^4$ cells/ml) for 30 min. The difference between initial and final diatom population densities, corrected for changes in a control, was used to estimate tunicate filtering rates as a function of size.

Macrobenthos

Ten core samples of 4.2 cm^2 were taken each month with a stick-mounted corer with a ball valve. A special frame on top of the tank allowed fairly precise positioning within the sediment area, and samples were randomized over the whole sediment area, although we avoided recently sampled areas. The corer was lowered slowly into the upper sediment, then pushed deeper with a rapid thrust (to avoid clogging by the deeper, more cohesive sediment), to ensure cores with a length of at least 6 cm. Each core was sliced into 0- to 2- and 2- to 6-cm layers and preserved in 4% formaldehyde buffered with hexamine. The preserved core strata were washed through 500-, 297-, and 44-μm standard soil sieves. All individuals retained by the 500- and 297-μm screens, except such meiofaunal groups as nematodes, ostracods, and copepods, were identified to species and enumerated as macrofauna. The meiofaunal taxa and the residue on the 44-μm sieve were enumerated as meiofauna.

At the end of the experiment, all the sediment in the tanks was washed through 6.4-mm sieves to recover and count the larger organisms that could not be adequately sampled with the monthly cores.

Meiobenthos

The sieved residues from the 0- to 2-cm layer of the 10 monthly faunal cores were used for the meiofauna analysis. All 10 cores were pooled and mixed, resulting in one composite sample per tank. The 2- to 6-cm layer was not included in the counts. Spot checks indicated that this section would have added 30 to 40% to the population of meiofauna, almost entirely nematodes and Foraminifera.

The samples were stained with rose bengal, and the whole 297-μm fraction was sorted. The finer fractions were divided into heavy and light fractions by decantation and subsampled with the subsampler described by Elmgren (1973) for the light material and a

subsampler similar to that described by Olsson (1975) for the heavy material. The subsample examined was at least $\frac{1}{8}$ of the material retained on a 200-μm sieve, $\frac{1}{40}$ of that on a 100-μm sieve, and $\frac{1}{200}$ of that on the fine sieve (44 μm). Taxonomic identification was generally to major group only.

Microbenthos

Sediment cores taken from control and oiled tanks were subdivided, and 40 cm^3 of sediment from the 0- to 2-cm layer was removed and homogenized. Diatom and ciliate population densities were determined by direct phase contrast microscopy.

RESULTS

Plankton

The small chain-forming centric diatom *Leptocylindrus minimus* dominated two of the three control tanks from early February through April, accounting for the elevated chlorophyll a levels in the controls (Fig. 1). No single species dominated the third control tank

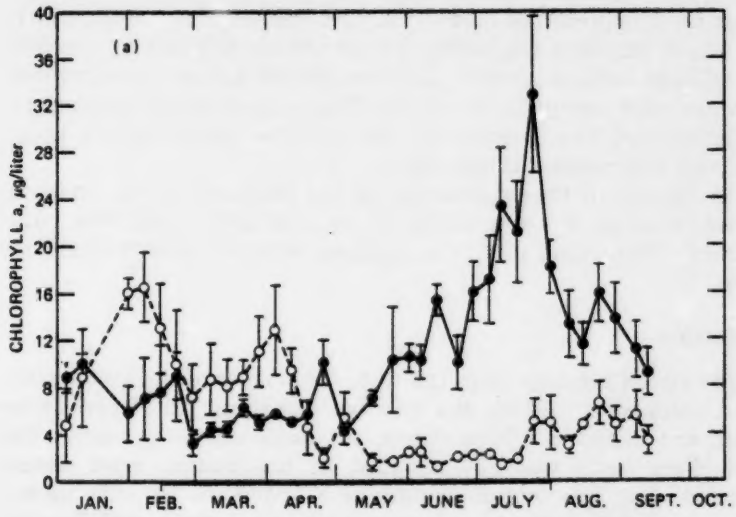

Fig. 1 (a) Phytoplankton biomass as chlorophyll a (micrograms per liter ± standard error) in the oiled tanks (●——●) and in the control tanks (○ – – ○). (b) Phytoplankton diversity as the average Shannon index ($\bar{H}$ ± standard error) of the three oiled tanks (●——●) and the three control tanks (○ – – ○). Points with no standard error bars are

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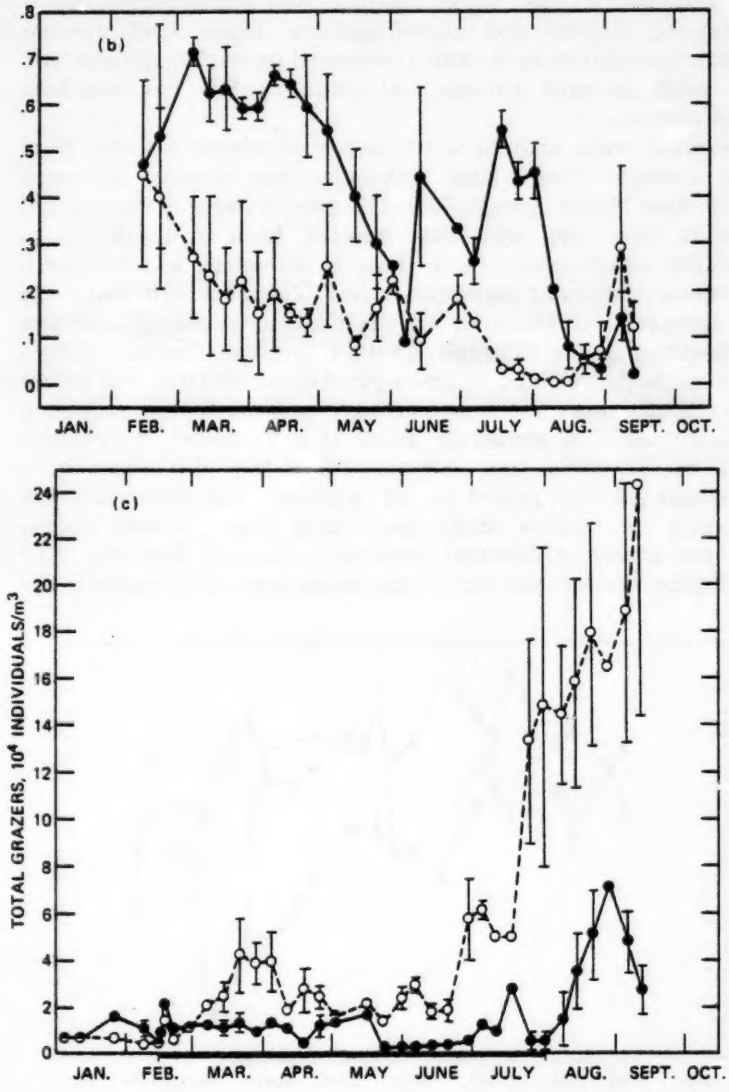


Fig. 1 (Continued)

averages of two or fewer tanks. (c) Average zooplankton concentration as total grazers per cubic meter ($\times 10^4$) for the three oiled tanks (●——●) and the three control tanks (○ – – ○). Standard error bars are shown for points only where they do not overlap. Heavy line on the time axis denotes the period of oil addition.

during this period; the water column was characterized by a succession of diatoms and microflagellates. From April through September the control tanks were dominated by microflagellates and several small pennate diatoms and exhibited low but relatively constant biomass.

The oiled tanks showed a succession of centric diatoms from January through June. Total phytoplankton biomass increased gradually from March through July. The great increase in chlorophyll biomass in late June and July resulted from a bloom of an unidentified nanoflagellate (1 to 2 μm in diameter), which numerically dominated all oiled tanks during July. The same form also made a brief appearance in the control tanks in late July, contributing to a slight elevation in the chlorophyll values. The nanoflagellate bloom in the oiled tanks declined in late July—August (starting well before the last oil addition); biomass decreased; and dominance shifted to microflagellates. The similarity index (Fig. 2) shows replicability between the phytoplankton communities of the oiled tanks to be high throughout the period of oil addition. The phytoplankton communities in control tanks were more heterogeneous during spring, and almost as different from each other as from the oiled tanks. During the summer the control tanks were as replicable as the

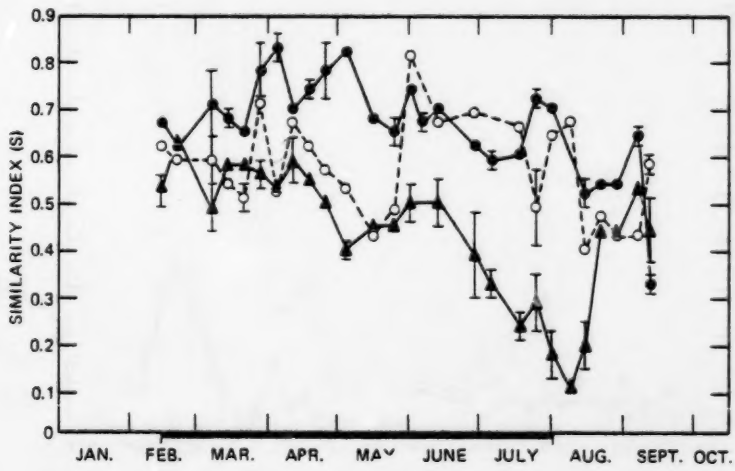


Fig. 2 Average similarity index (S ± standard error) for a comparison of all the control tanks (○ – – ○) with each other, all oiled tanks with each other (●——●), and all combinations of control tanks compared with all oiled tanks (▲——▲). Error bars are plotted only on points where they do not overlap with another data point. Heavy line on the time axis denotes the period of oil addition.

oiled tanks, but species composition in the two treatments diverged radically. After oil addition was stopped, the phytoplankton communities in the two treatments became indistinguishable within 3 to 4 weeks, despite continued differences in biomass (Fig. 1).

The Shannon diversity index [Fig. 1(b)] responded rapidly to the oil additions, increasing in the oiled tanks and declining in the controls. Both diversity and evenness of phytoplankton were greater in the tanks treated with oil. (This difference was largely a result of higher abundance of several centric diatom species in the oiled tanks.) The nanoflagellate found in the oiled and control tanks in July was not included in diversity calculations since, with the methods used, it was difficult to discriminate clearly between heterotrophic and autotrophic flagellates that occurred simultaneously and were of the same size. The collapse of the nanoflagellate bloom in the oiled tanks was accompanied by a rapid decrease in diversity; thus by late August both treatments had similar, very low diversities caused by a dominance by microflagellates. Total inorganic nitrogen concentrations in the oiled tanks were less than 1 μg atom/liter throughout the experiment [Fig. 3(a)], whereas the control tanks showed increased levels after the termination of the *L. minimus* bloom in late April.

Silicate [Fig. 3(c)] and phosphate [Fig. 3(b)], on the other hand, displayed a similar seasonal cycle and concentration range in oiled and control tanks. The main difference was a delay of over a month of the spring increase in the oiled tanks, probably because of the persistence of a diatom population in those tanks.

Zooplankton population densities [Fig. 1(c)] were initially very low in both oiled and control tanks in comparison with levels in Narragansett Bay. Within about a month after the first oil addition, there were clear differences between oiled and control tanks, with lower total population densities in the oiled tanks. A large proportion of the total zooplankton population in both groups was harpacticoids, however, and it was not until May that the control tanks acquired a sizable population of zooplankton similar in composition to that in the bay. *Acartia clausi* appeared first, followed by *Pseudodiaptomus coronatus* and *Oithona* sp. in July and August. There was some increase in total zooplankton densities in the oiled tanks in August after oil addition had ceased, but control levels were never attained.

Benthos

The tunicate *Molgula manhattensis* was not observed in the oiled tanks but occurred in the control tanks in densities varying with

location in tanks and between tanks. On the basis of in-tank photographs taken in July 1977, we used an estimate of 500 to 1500 animals per tank for further calculations. After taking a few samples from the tanks, we assumed a mean wet weight per individual of 1 g. Filtering-rate measurements were 325 ml animal^{-1} hr^{-1} for a 1-g animal.

The density of smaller macrofauna, sampled by the benthic cores, tended initially to be slightly higher in the oiled tanks [Fig. 4(a)]. After oil additions started, macrofauna decreased in the oiled tanks (starting in April), whereas density in the control tanks increased. By June, the difference between oiled and control tanks was statistically significant (±2 standard errors of the mean did not overlap). The decrease in abundance in the oiled tanks was mostly

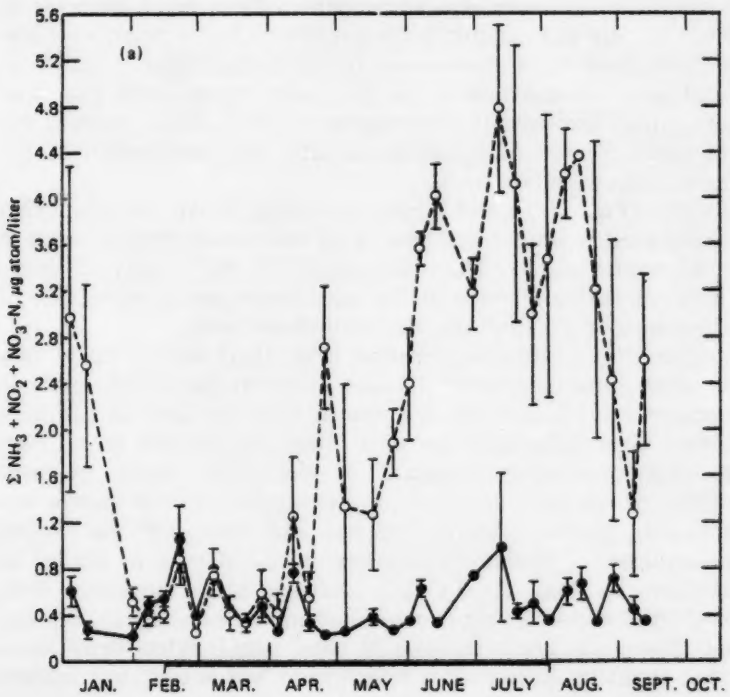
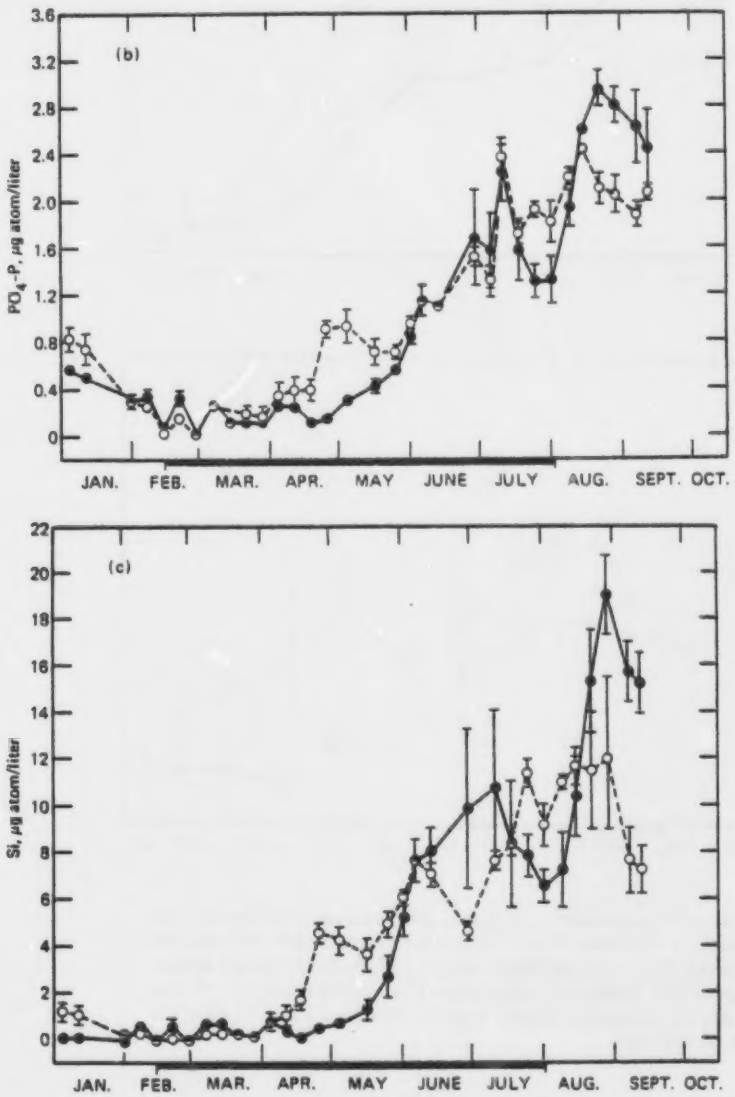


Fig. 3 Average concentration of total inorganic nitrogen (a), dissolved reactive phosphate (b), and silicate (c) in microgram atoms per liter (± standard error) in the three oiled tanks (●——●) and the three control tanks (○ — — ○). Heavy line on the time axis denotes the period of oil addition.

(Figure continues on following page.)

caused by the rapid disappearance of the normal numerical dominant, the small polychaete *Mediomastus ambiseta*. During the rest of the summer, macrofauna populations declined in both oiled and control tanks. For two of the three control tanks, macrofaunal



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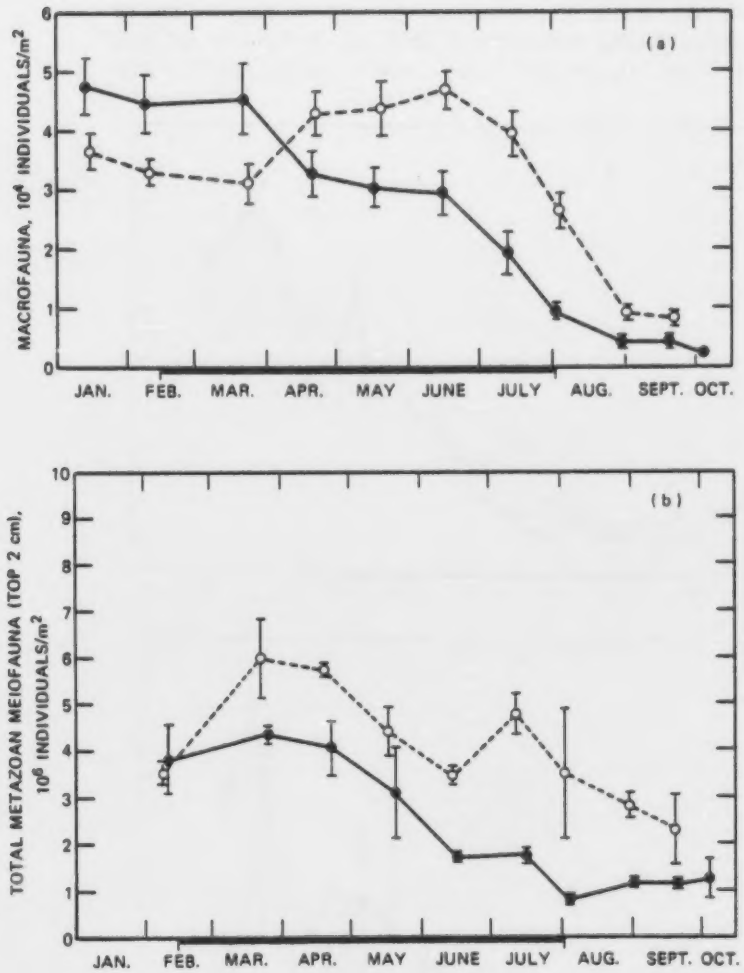

Fig. 4 Seasonal abundance of total macrofauna (individuals per square meter ± standard error) for the oiled tanks (●——●) and the control tanks (○ – – ○). (a) Macrofauna (10^4 individuals per square meter). (b) Total metazoan meiofauna (10^6 individuals/m^2) in the upper 2 cm of sediment. Heavy line on the time axis denotes the period of oil addition.

TABLE 1

LARGE MACROFAUNA IN MERL TANKS AT END OF EXPERIMENT, SEPTEMBER TO OCTOBER 1977

Macrofauna	Mean of three control tanks, g wet weight	Mean of two oiled tanks, g wet weight
Suspension feeders	627.1	14.5
Deposit feeders	39.7	23.0
Carnivores	178.4	41.4
Total	845.2	78.9

populations remained clearly higher than in the oiled tanks, even after oil additions had ceased. There was no discernable recovery of the macrofauna of the oiled tanks; in fact, the population density continued to decline.

The large macrofauna recovered from the tanks at the end of the experiment showed over 10 times higher biomass in the control tanks than in the oiled tanks (Table 1). Most of the difference was caused by the almost total absence of suspension-feeding animals in the oiled tanks. Not a single large suspension-feeding bivalve remained alive in the oiled tanks, whereas over 90% of the biomass in the controls was a single species, *Pitar morrhuana* (specimens 20 to 48 mm in length).

The difference in wall fouling at the end of the experiment was less dramatic (Table 2), with just over twice the biomass in the control tanks. *Anomia simplex*, *Crepidula fornicata*, and *C. plana* dominated the control tanks, and serpulids were the most important group in the oiled tanks. Very small worm tubes and Bryozoa could not be quantitatively dislodged from the walls, and tunicates that had been dislodged during removal of the sediment container were not included in the total figures.

Initial densities of meiobenthic populations in the oiled and control tanks were virtually indistinguishable from each other [Fig. 4(b)], a similarity that extended also to the two dominant taxonomic groups, the nematodes and the harpacticoids. After the oil additions the total meiofaunal abundances were always higher in the control than in the oiled tanks, the difference being statistically significant for all months except March and May [two-tailed rank—sum test, $P = 0.1$, Dixon and Massey (1957)]. Initially the effect of oil was clearest on the nematodes, whose numbers increased considerably in all control tanks from February to March but

TABLE 2

WALL EPIFAUNA IN MERL TANKS AT END OF EXPERIMENT, SEPTEMBER 1977

Epifauna	Mean of two control tanks, g dry weight	One oiled tank, g dry weight
Anomia simplex	43.8	14.0
Crepidula fornicata and *C. plana*	69.2	16.3
Others (serpulids, barnacles, etc.)	6.3	24.9
Total	119.3	55.2

changed little in the oiled tanks. The nematode abundance remained significantly higher (rank—sum test, $P = 0.1$) in the control tanks throughout the experiment, with the exception of May, when one oiled tank had an unusually high count. The harpacticoids did not show statistically significant differences until May, when there were more copepodites and adults in the controls, and total counts, including nauplii, were significantly higher only from June to early August (rank—sum tests, $P = 0.1$). The meiofauna population in the control tanks peaked in March and April, with levels near those in Narragansett Bay [6 to 8 million/m^2 in the upper 2 cm in March and April 1978 (Elmgren and Rudnick, unpublished data)] and then decreased, except for a small peak in July. The meiofaunal populations in the oiled tanks showed a similar decreasing trend but were always at lower densities. The harpacticoid populations responded rapidly to the cessation of oil addition in early August. By mid-September there were four times as many harpacticoids in the formerly oiled tanks as in the control tanks, a statistically significant difference (rank—sum test, $P = 0.1$). Other meiofaunal groups showed only weak signs of a recovery.

Before the start of the experiment, oiled and control tanks showed similar population densities of benthic ciliates [Fig. 5(a)] and diatoms [Fig. 5(b)]. By June ciliate and diatom densities were greater in the oiled tanks, a difference which persisted throughout the experiment. Other microbenthos, including flagellates and Foraminifera, showed increased population density during the period of oil exposure. Analyses of meiofauna samples also confirmed these patterns, with significantly higher densities of ciliates in the oiled tanks by March and of Foraminifera by May (rank—sum test,

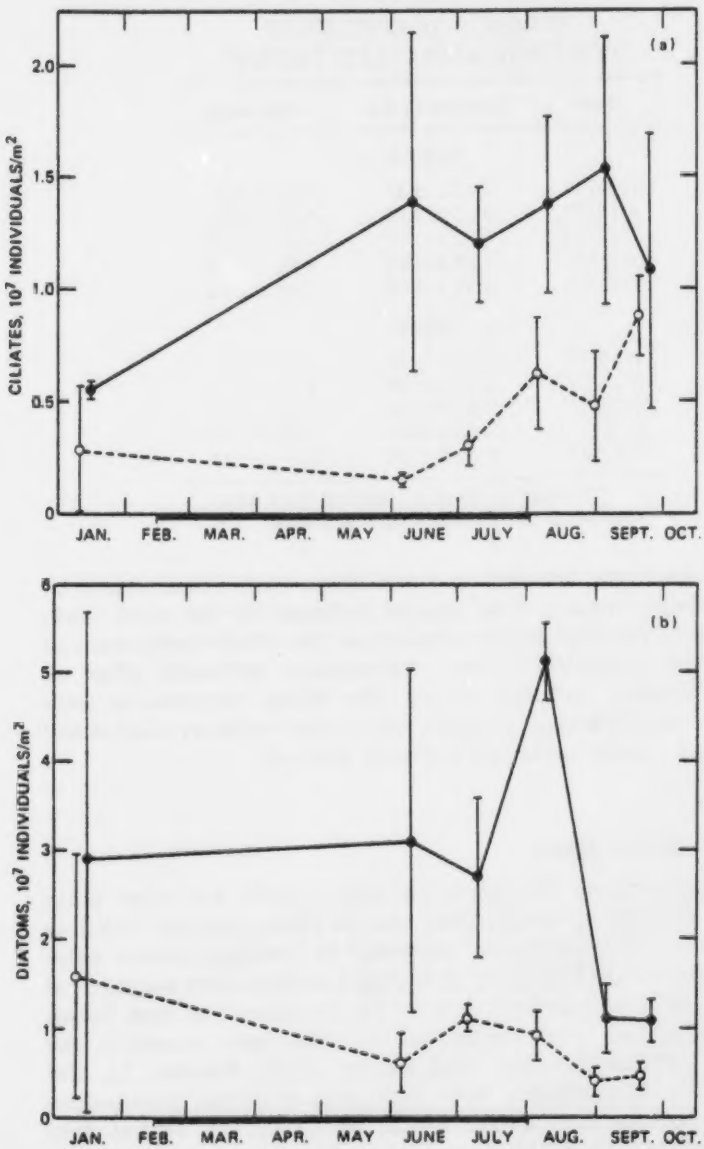

Fig. 5 Comparison of benthic ciliates (a) and benthic diatoms (b) (10^7 individuals/m^2 ± standard error) in the three oiled tanks (●——●) and the three control tanks (○ – – ○). Heavy line on the time axis denotes the period of oil addition.

TABLE 3
NUMBER OF SPECIES IN CONTROL AND OILED TANKS*

Date	Control tanks	Oiled tanks
	Diatoms	
1/15/77	7.33 ± 5.36	10.5 ± 9.5
6/13/77	3.33 ± 0.88	5.00 ± 0.0
7/13/77	4.33 ± 0.67	5.33 ± 1.03
8/1/77	4.33 ± 0.67	8.66 ± 2.18
8/31/77	3.33 ± 0.66	4.66 ± 0.34
	Ciliates	
1/15/77	1.33 ± 1.33	3.0 ± 2.0
6/13/77	1.33 ± 0.28	3.50 ± 0.71
7/13/77	3.66 ± 2.18	7.67 ± 0.88
8/1/77	3.00 ± 0.57	7.33 ± 2.34
8/31/77	3.00 ± 1.52	5.33 ± 1.45

*Average number of species from three samples per treatment ± standard error.

$P = 0.1$). Both ciliate and diatom populations were characterized by higher diversity, measured as species richness, in the oiled tanks (Table 3), and the species composition of the ciliate component of the microbial community was dramatically different after oil exposure. Trophic patterns among the ciliate populations were different in control and oiled tanks, with more predatory ciliates and diatom-eating ciliates in the tanks treated with oil.

DISCUSSION

The Plankton–Benthic System

The most striking difference between control and oiled tanks after a few months of oil additions was the phytoplankton bloom in the oiled tanks. This contrasted markedly to the much clearer water of the control tanks [Fig. 1(a)]. Although literature data suggest that stimulation of phytoplankton growth by oil sometimes does occur, this is generally at lower concentrations than were present in the oiled tanks (Prouse, Gordon, and Keizer, 1976; Parsons, Li, and Waters, 1976). Experiments with tank phytoplankton populations and in-tank production measurements before and for several days after oil addition failed to show either significant stimulation or long-term reduction of turnover rates at tank oil levels (Vargo, unpublished data). Therefore direct stimulation of the phytoplankton by oil addition was not responsible for the observed bloom.

TABLE 4

ESTIMATED TOTAL FILTERING CAPACITY (JULY)

	Control tanks		Oiled tanks	
	liters/day	%	liters/day	%
Zooplankton	260–520	2–4	26–65	0.2–0.5
Wall tunicates	3,912–11,736	30–90		
Other wall fouling	1,728	13	792	6
Benthos	3,888	30	16	0.1
Total	9,788–17,872	75–137	834–873	6–7

Nutrient data indicate continuous limitation by nitrogen in the oiled ecosystems [Fig. 3(a)], whereas in the control systems neither nitrogen, phosphorus, nor silicate seemed likely to limit production after mid-April (Fig. 3). The lower biomass in the control tanks clearly must have some other explanation.

Zooplankton sampling clearly shows higher zooplankton abundances in the control tanks, but the difference is not very dramatic until late July, long after the bloom has developed in the oiled tanks. Estimates of zooplankton filtering rate (Heinle, unpublished data, Table 4) show the expected higher rate in control tanks, but the difference is not very large. When epifaunal filter feeders growing on the tank wall and infaunal suspension feeders in the mud are also taken into account, the difference becomes very drastic. No tunicates were observed in the oiled tanks (a few might have passed unnoticed, but not a large population), and suspension feeders were the most negatively affected trophic group within the benthos (Table 1). There was also a difference in wall-fouling growth other than tunicates (Table 2). Using rough approximations, we have attempted to estimate the filtering rate of these populations (Table 4). Zooplankton filtering rate was calculated from the mean zooplankton biomass for each tank group and a daily requirement, as carbon, of 20% of body weight for *Acartia tonsa*. A chlorophyll-to-carbon ratio of 50 : 1 was used to calculate particulate carbon, and it was assumed that zooplankton carbon was 50% of dry weight. Tunicate filtering rate was determined experimentally (see section on results). Dry weights of the wall epifauna were measured at the end of the experiment. Since *Anomia simplex*, *Crepidula fornicata*, and *C. plana* were fairly large, it was assumed that growth since the end of oil addition (Aug. 1, 1977) could be ignored. This compensated, to some extent, for the undersampling of some fauna, especially crustose Bryozoa. The total dry weight was assumed to be 10% dry

tissue weight, and a filtering rate of 100 ml min^{-1} g^{-1} of dry tissue was assumed to be representative for the organisms present. The filtering rate was estimated from data in Walne (1972) and Winter (1978). Mean abundance, wet and dry weights of macrofauna filter feeders, was measured at the termination of the experiment (Grassle and Grassle, unpublished data). Filtering rates were estimated from the mean dry weights of each species and data from Walne (1972). Although large uncertainties are involved in these estimates, the total grazing pressure in the control tanks is about an order of magnitude greater than in the oiled tanks. This difference is large enough to explain the lower phytoplankton biomass in the control tanks.

This type of algal bloom after reduction or loss of grazers was not entirely unexpected; it has been observed several times in microcosm research (e.g., Taub, 1976; Taub and Crow, 1978), but it has generally involved only the plankton system rather than the type of bentho—pelagic interaction observed in the MERL tanks.

A more surprising aspect of the phytoplankton results was the higher diversity observed in a system that was both stressed and had lower grazing pressure. Stress is generally considered to decrease diversity (Copeland and Bechtel, 1971; Borowitzka, 1972), and, from the work of Paine (1966), predation (grazing) has generally been considered a means of allowing coexistence of more species and hence greater diversity.

The nonequilibrium model of Caswell (1978) may resolve some of the difficulty, however. Each tank could be considered a single almost-closed cell, and, with heavy continuous grazing, diversity will decrease. The lower grazing rates of the oiled tanks allow more species to maintain themselves, however. The bay, on the other hand, would be a fairly heavily grazed system consisting of a large number of open cells that constantly exchange species. In accordance with this theory, the bay has even higher diversity than the oiled tanks (Vargo, unpublished data). High predation rates in the control tanks can be compared with chemostats run at a high dilution rate (1/day or more), and, not surprisingly, all but the fastest growing species are flushed out of the system, with a microflagellate population as the dominant survivors.

The oil seems to be a far less important controlling factor than the high filtering rate on the phytoplankton community and its diversity.

Benthic System

A second example of stress and trophic interactions occurred in the benthic community, where the effect of oil additions was

dramatic. The abundances of all metazoan bottom fauna, except *Nereis virens*, decreased after 1 to 2 months of oil addition. Concomitantly, several types of benthic unicellular microbiota increased in abundance [Fig. 5(a)], particularly ciliates [Fig. 5(a)] and diatoms [Fig. 5(b)]. The diatoms flourished despite the lowered light level at the sediment surface (normally 1% or less of surface intensity in the control tanks) which resulted from the phytoplankton bloom in the water column.

No evidence for oil-mediated stimulation of growth in either metazoan or unicellular bottom fauna or flora is available to our knowledge. Winters, Van Baalen, and Nicol (1977) reported either inhibition or no effect of several types of oil and/or pure hydrocarbon compounds on two pennate diatoms (*Cylindrotheca* sp. and *Amphora* sp.). It is possible, of course, that dissolved inorganic material from both the oil additions and degradation of bottom fauna increased in the upper layer of sediment and contributed to the available nutrient supply of the benthic diatoms—some of which are known to grow heterotrophically (Lewin and Lewin, 1960). Nitrogen, although probably limiting biomass in the water column, need not be a limitation in the benthic surface layer since diffusion of nitrogen and phosphorus from sediment pore water is known to support diatom growth at this surface (Admiraal, 1977).

The most probable causes for the increase in microfauna and diatoms were decreased ingestion by sediment-feeding macrofauna and decreased predation and grazing by meiofauna. This allowed new food chains to develop, with increased numbers of diatom-eating ciliates and predatory ciliates. Similar patterns of diatom–ciliate population dynamics have been observed by Admiraal (1977) in unperturbed laboratory microcosms.

As in the water column, the increased diversity in two compartments in the benthic community under a stressed situation and decreased predation was not intuitively obvious. Higher populations of predators and grazers in the control tanks maintained a more "normal" (or at least unchanged) level of trophic interactions than in the "stressed" tanks, where, through the action of the oil additions in removing predators, both the populations and the diversity of two microorganism compartments increased.

CONCLUSIONS

The complexity of natural ecosystems precludes accurate prediction of the effects of a stress without experimentation. Some effects of perturbation might be predictable from accepted theory,

but validation of such predictions is required. Other unexpected results may also occur, thus demonstrating the need for further studies before explanations are attempted. Time scales for such studies become important. It is unlikely that the examples described here would have been seen during a short-term (1- to 2-month) study.

Our studies support the microcosms approach as one of the most promising ways to study ecosystem function. It is only in microcosms such as those found at MERL, which contain both major elements of shallow-water productive coastal ecosystems, that the interactions between plankton and benthos can be studied and the effects of stress (especially pollutants) on the entire system can be investigated.

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